

Collembola, Springtails

J.-M. Betsch

Translated from the original French

by L. Ramandimbilahatra and S. M. Goodman

Collembola is one of the most ancient hexapod groups known today. Its first appearance in the fossil record is in the mid-Devonian "old red sandstones" of Scotland, and at that time it was already typical of present-day families. Thus, its origin can be considered much more ancient. The earliest information on Malagasy Collembola is the descriptions of three species of Isotomidae, Entomobryidae, and Symphypleona (Börner 1907). Subsequently, Denis (1929, 1947), Delamare Deboutteville (1948, 1950), Delamare Deboutteville and Massoud (1964), and Massoud and Betsch (1966c) named several other species based on material obtained from some general insect collections.

Starting in 1965, I made six visits, totaling 30 months of field work, prospecting microarthropod fauna (especially Collembola) at a large number of sites (fig. 8.15 and table 8.20). Field techniques included soil, litter, and moss sampling and bush threshing. This sizable amount of material was the basis for detailed studies of Symphypleona by Betsch (1970, 1974a,b,c, 1975, 1977, 1980, 2000a,b) and Betsch and Waller (1996), as well of Poduromorpha Neanurinae by Cassagnau and Deharveng (1980) and Cassagnau (1996). Further, one species of Entomobryomorpha was described, as well as a new genus of the new subfamily Microfalculinae (Massoud and Betsch 1966a,b; Betsch and

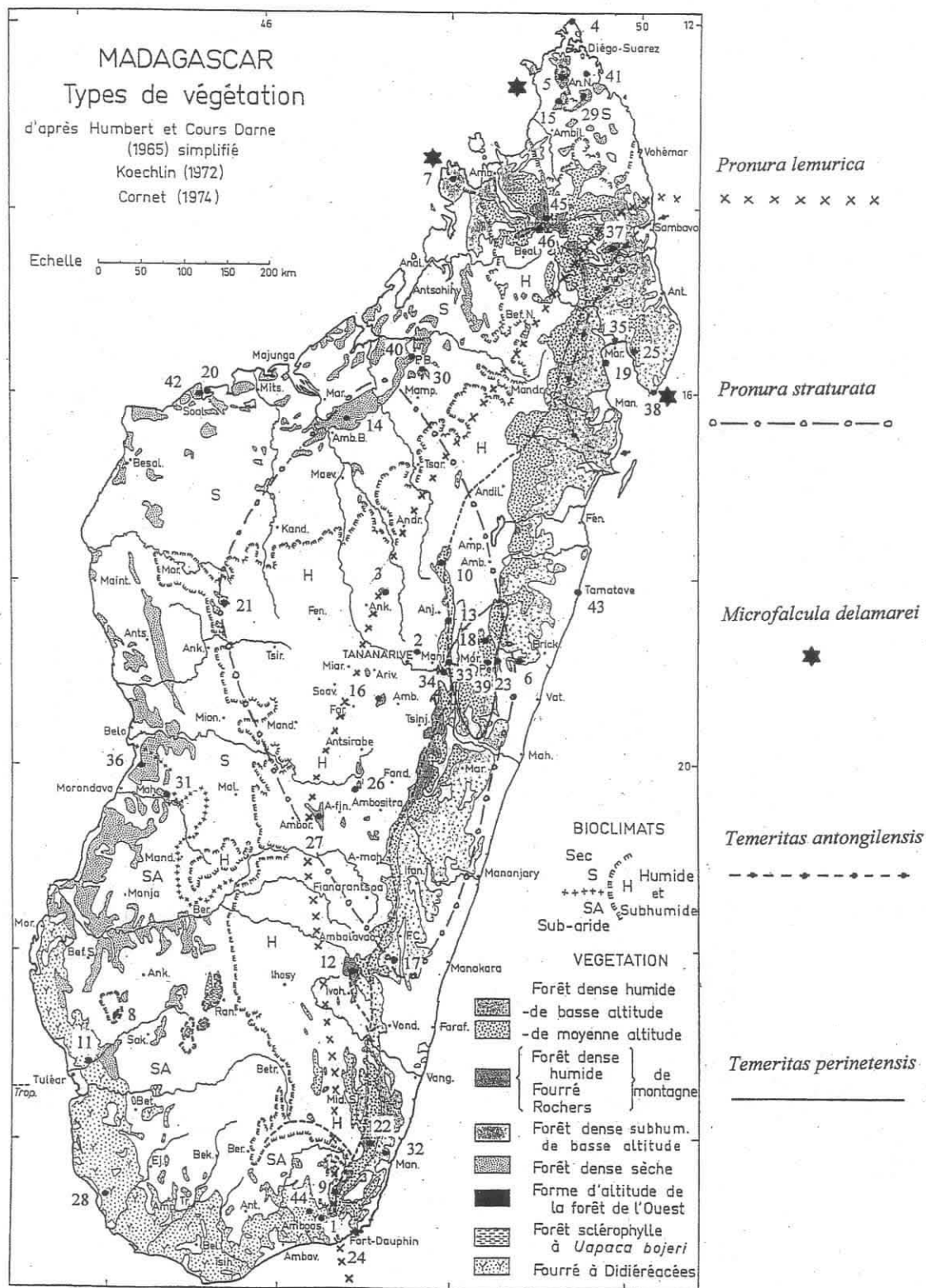


Figure 8.15. Collection sites of Malagasy Collembola. The numbering system follows the localities presented in table 8.20. The geographic distribution of five species is also presented.

Table 8.20. Sites surveyed on Madagascar for Collembola

Site number ¹	Site	Species found at site
1.	Amboasary, PN d'Andohahela (parcel 2)	<i>Richardsitas najtae</i>
2.	Ambohimanga	<i>Pronura setimigrans</i> , <i>P. straturata</i>
3.	Ambohitantely	<i>Pronura lemurica</i> , <i>P. straturata</i> , <i>Temeritas ambohitantelensis</i>
4.	Ambre (Cap d' -)	<i>Oudemansia dubia</i>
5.	Ambre (Montagne d' -)	<i>Microfalcula delamarei</i> , <i>Temeritas ambrensis</i>
6.	Ampasimbe	<i>Temeritas ampasimbensis</i>
7.	Ampasindava (peninsula)	<i>Microfalcula delamarei</i>
8.	Analavelona (massif)	<i>Pronura sphaeroculata</i>
9.	Andohahela (massif)	<i>Paleonura anosyennica</i> , <i>P. plumosa</i> , <i>Pronura lemurica</i>
10.	Andranobe (forest)	<i>Temeritas andranobensis</i>
11.	Andranohinalahy	<i>Rastriopes amphygia</i>
12.	Andringitra (massif)	MEF-MscPF: <i>Afrobella mamillata</i> , <i>A. scoparia</i> , <i>Pronura anjavicola</i> , <i>P. elegans</i> , <i>P. madagascariensis</i> , <i>P. lemurica</i> , <i>P. straturata</i> ; MPT: <i>Anjavidiella andoharianensis</i> , <i>A. andringitrensis</i> , <i>A. anjavidiavensis</i> , <i>A. vohidrayensis</i>
13.	Anjozorobe (southeast of -; Vanjamanitra)	<i>Pronura lemurica</i> , <i>P. straturata</i> , <i>Temeritas anjozorobensis</i>
14.	Ankarafantsika	<i>Pronura straturata</i> , <i>Temeritas ankarafantsikensis</i>
15.	Ankarana (karstic massif)	<i>Temeritas mahorensis</i> , <i>T. sahafarensis</i>
16.	Ankaratra (massif)	MEF: <i>Bourietillitas imerinensis</i> , <i>Papirinus ankaratrensis</i> , <i>Pronura lemurica</i> , <i>Salina nigra</i> , <i>Sphyrotheca madagascariensis</i> ; MPT + MS: <i>Anjavidiella ankaratrensis</i> , <i>Salina trilineata</i> , <i>Vatomadiella pauliani</i>
17.	Ankarimbelo	<i>Lepidocyrtinus voeltzkowi</i>
18.	Ankarongambe (50 km north of Andasibe)	<i>Pronura lemurica</i> , <i>P. straturata</i> , <i>Travura betsi</i> , <i>Temeritas perinetensis</i>
19.	Antongil (Baie d' -)	<i>Axelsonia thalassophila</i> /marine, <i>Temeritas antongilensis</i> /terrestrial
20.	Baly (Baie de -)	<i>Archisotoma brucei</i>
21.	Bongolava	<i>Paleonura coalescens</i> , <i>Pronura straturata</i>
22.	Chânes Anosyennes, east slope	<i>Paleonura anosyennica</i> (1100–1900 m), <i>Pronura pumilio</i> (1900 m), <i>Temeritas anosyennensis</i> (100–1300 m)
23.	Fanovana	<i>Travura betsi</i>
24.	Fort Dauphin (= Tolagnaro)	<i>Friesea petiti</i> , <i>Oudemansia petiti</i>
25.	Iaraka (forest)	<i>Temeritas iarakensis</i>
26.	Ibity Massif, southern slopes	<i>Madecassiella ibityensis</i> , <i>Vatomadiella descarpentriesi</i>
27.	Itremo Massif	<i>Pronura lemurica</i> , <i>P. straturata</i> , <i>Vatomadiella peyeri</i>
28.	Mahafaly Plateau	<i>Parabourletella mahafalensis</i>
29.	Mahory (forest)	<i>Temeritas mahorensis</i> , <i>T. sahafarensis</i>
30.	Mampikony (between N and Port Bergé)	<i>Massoudia griveaudi</i> , <i>Temeritas bergensis</i>
31.	Manamby (forest)	<i>Pronura prima</i>
32.	Manantenina (Analava Forest)	<i>Pronura lemurica</i> , <i>Temeritas mananteninensis</i>
33.	Mandraka (la -)	<i>Salina insignis</i> , <i>Temeritas perinetensis</i>
34.	Mantasoa (east of -; Andrangoloaka)	<i>Temeritas mantasoensis</i>
35.	Maroantsetra	<i>Bovicornia cf. greensladei</i> /terrestrial, <i>Sminthurides sensillatus</i> /interstitial
36.	Marofandilia	<i>Paulianitas viettei</i> , <i>Richardsitas griveaudi</i>
37.	Marojeiy Massif	<i>Pronura caeca</i> (1900–2060 m), <i>Pronura lemurica</i> (1300–2070 m), <i>Temeritas marojezensis</i> (600–1300 m), <i>T. antongilensis</i> (<600 m)
38.	Masoala (Cap -; Nosy Behentona)	<i>Microfalcula delamarei</i>
39.	Périnet = RS d'Analamazaotra	<i>Pronura lemurica</i> , <i>Salina milloti</i> , <i>Temeritas perinetensis</i> , <i>T. ampasimbensis</i>
40.	Port-Bergé (between Mampikony and -)	<i>Massoudia griveaudi</i> , <i>Temeritas bergensis</i>
41.	Sahafary (forest)	<i>Temeritas sahafarensis</i>

(continued)

Table 8.20. (continued)

Site number ¹	Site	Species found at site
42.	Soalala (Tongahibe Forest)	<i>Temeritas soalalensis</i>
43.	Toamasina	<i>Seira jacobsoni</i> , <i>S. pseudocoerulea</i>
44.	Tranomaro	<i>Paleonura anosyennica</i>
45.	Tsaratanana, northeast slope	<i>Temeritas tsaratananensis</i>
46.	Tsaratanana, south slope	<i>Pronura laminata</i> , <i>Zebulonia massoudi</i>

¹ Site number as shown on map in fig. 8.16.

NOTE: See table 8.22 for vegetation and bioclimatic codes.

Massoud 1968, 1973). This taxonomic work on Malagasy Collembola brought the total number of described species to 69, distributed among 25 genera. There are still many species to be described within at least 11 additional genera, including 3 new genera of Neanurinae (Betsch and Cassagnau 1996) and 9 Holotropical genera (*Denisiella*, *Collophora*, *Afrosminturus*, *Pararrhopalites*, *Calvatomina*, and *Papirioides*) or genera with broader distributions (*Sphaeridia*, *Sminthurinus*, and *Stenognathellus*) among the Symphypleona (Betsch 1980).

The study of the Malagasy Collembola fauna is incomplete, in part because of the lack of specialists. It is certain that less than 20% of the Malagasy Collembola fauna is known, which is why this group has never been the subject of a volume of the *Faune de Madagascar*. However, there have been studies of patterns of geographic and ecological distribution and of speciation in these organisms (Betsch 1971, 1980, 2000a; Betsch and Cassagnau 1996).

Endemism

The 69 species described represent only a fraction of the island's total Collembola diversity. Since this group can occupy all the biotopes of an ecosystem, some of which remain entirely unexplored (e.g., canopy, epiphytes, and suspended soil in forests), it is likely that the description stage of the Malagasy species will remain incomplete for several decades to come. The majority (64 of 69 species) of these animals are endemic to Madagascar (table 8.21).

At a generic level, endemism is found in 10 of the 27 genera on Madagascar, or 37%, and this rate varies among the groups: Entomobryomorpha, 17%; Poduromorpha, 0% (but potentially 33% with the 3 genera to be created); Symphypleona 60% (39% if we include all the present genera, but not including several as yet undescribed species).

Further, there are a few endemic subfamilies (table 8.21), which include Microfalculinae Massoud and Betsch, 1966, with a monotypic genus—a very isolated subfamily within the Entomobryomorpha, upgraded to the rank of

family by Szeptycki (1979); and Parabourletiellinae Betsch, 1974, part of the Symphypleona: Bourletiellidae lineage with a notable radiation (six genera living in very different environments).

A comparison of the diversity and endemism of Malagasy Collembola with those of other tropical areas of the world poses several problems. Foremost is difficulty in comparing sampling techniques. In certain regions of the world methods for sampling (traps, soil or litter sifting, fauna extraction by drying) are not widely used, and comparisons of species richness are accordingly difficult to make.

Geographic and Ecological Distributions

The Collembola are members of the microarthropod fauna that is associated with soil and associated habitats (e.g., litter, mosses). The occurrence of these animals on Madagascar is dependent on geological history and on the evolution that the lineages have undergone since the breakup of Gondwanaland. However, their modern distribution on the island depends on ecological criteria.

Climate/Rainfall, Temperature, and Substratum Hygrometry

Soil-dwelling (hypogeous) Collembola have remained dependent on soil conditions, unlike the aboveground (epigeous) forms, which have developed strategies allowing them to adapt themselves to less buffered hydric and thermal conditions. Two limiting factors play an essential role in delimiting their distributions—the long-term average minimum of the coldest month and the annual hydric deficit (see bioclimatic coding, table 8.22). For example, the distribution of the Poduromorpha: Neanurinae genera *Pronura* and *Paleonura* shows at least three species that have a wide ecological distribution, associated with their stable hypogean ecology in forest ecosystems. *Pronura lemurica* and *P. straturata* are two species with broad distributions (fig. 8.15). *Paleonura anosyennica* (stations 9 and 44) has a

Table 8.21. Checklist of known Malagasy springtails (Collembola)

Taxon	Status	Distribution — station within Madagascar	Elevation (m)	Vegetation	Bioclimate
Poduromorpha					
Family Neanuridae					
Subfamily Frieseinae					
Genus <i>Friesea</i> Dalla Torre, 1895					
<i>F. petiti</i> (Delamare Deboutteville and Massoud, 1964)	Endemic	Southeast/Tolagnaro, beach	~0	Interstitial	Hh/c
Subfamily Pseudachorudinae					
Genus <i>Oudemansia</i> Schött, 1893					
<i>O. petiti</i> Delamare Deboutteville and Massoud, 1964	Endemic	Southeast/Tolagnaro, beach	~0	Interstitial	Hh/c
<i>O. dubia</i> Denis, 1947	Endemic	North/Cap d'Ambre	~0	Coral reef	S3/a
Subfamily Neanurinae					
Genus <i>Travura</i> Cassagnau and Deharveng, 1980					
<i>T. betschi</i> Cassagnau and Deharveng, 1980 (type species)	Endemic	Central-east/Ankarongambe and Fanovana Forests	900	MFMA	Hp-Hh/c
Genus <i>Paleonura</i> Cassagnau, 1986					
<i>P. anosyennica</i> Cassagnau, 1996	Endemic	Southeast/east slopes, Anosyennes Mountains	1100–1900	MFMA–MEF DET	Hp/f–M
		+Southeast/Tranomaro	160		sA1/c
<i>P. coalescens</i> Cassagnau, 1996	Endemic	Subwest/Bongolava	1200	MFMA	sH2/d–e
<i>P. plumosa</i> Cassagnau, 1996	Endemic	Southeast/PN d'Andohahela (parcel 1)	1750	MEF	sH1/f
Genus <i>Pronura</i> Delamare Deboutteville, 1953					
<i>P. anjavicola</i> Cassagnau, 1996	Endemic	Central/PN d'Andringitra-Anjavidilava	1800–1900	MEF	Hh/f–fM
<i>P. caeca</i> Cassagnau, 1996	Endemic	Northeast/PN de Marojejy	1900	MEF	Hp/f
<i>P. elegans</i> Cassagnau, 1996	Endemic	Central/PN d'Andringitra-Anjavidilava	2000	MscPF	Hh/fM
<i>P. laminata</i> Cassagnau, 1996	Endemic	North/Tsaratanana, south slope	1600–2000	MFMA	sH1/fM
<i>P. lemurica</i> Cassagnau, 1996	Endemic	East + central/east slope to mountain	0–2200	MFLA to MPT	Hp-sH1/a to f
<i>P. madagascariensis</i> Cassagnau, 1996	Endemic	Central/PN d'Andringitra central + south	1700–2550	MEF–MPT	sH1/f-M
<i>P. prima</i> Cassagnau, 1996	Endemic	West/Manamby Forest	~100	DDF	S3–sA1/c
<i>P. pumilio</i> Cassagnau, 1996	Endemic	Southeast/east slope, Anosyennes Mountains	1900	MEF	Hh/fM
<i>P. setimigrans</i> Cassagnau, 1996	Endemic	Central/Ambohimanga	1400	MFMA degraded	sH1/e
<i>P. sphaeroculata</i> Cassagnau, 1996	Endemic	Southwest/Analavelona Massif	1250	MFMA–ShFMA	sH1–sH2/e
<i>P. straturata</i> Cassagnau, 1996	Endemic	Central: East cliff to mountain	900–1950	MFMA–MEF	Hh–sH2/d–fM
		+West/Ankarafantsika	100	DDF	S2/a
Genus <i>Afrobella</i> Cassagnau, 1983					
<i>A. mamillata</i> Cassagnau, 1996	Endemic	Central/PN d'Andringitra	1800–2000	MEF–MscPF	sH1/f–fM
<i>A. scoparia</i> Cassagnau, 1996	Endemic	Central/PN d'Andringitra	1800–2080	MEF to MPT	Hh–sH1/f to M
Entomobryomorpha					
Family Isotomidae					
Genus <i>Axelsonia</i> Börner, 1906					
<i>A. thalassophila</i> Börner, 1907	Endemic	Northeast/Baie d'Antongil, beach	~0	In empty shells	Hp/a

(continued)

Table 8.21. (continued)

Taxon	Status	Distribution — station within Madagascar	Elevation (m)	Vegetation	Bioclimate
Genus <i>Archisotoma</i> Axelson, 1912					
<i>A. brucei</i> (Carpenter, 1907)	+New Zealand	West/Baie de Baly, beach	~0	In sand at low tide	S2/b
Family Entomobryidae					
Genus <i>Salina</i> MacGillivray, 1894					
<i>S. insignis</i> (Handschin, 1928)	+Java	Central/La Mandraka	1200–1250	MFMA	Hh/e
<i>S. milloti</i> Delamare Deboutteville, 1948	Endemic	Central-east/Réserve Spéciale d'Analamazaotra	928	MFMA	Hh/d
<i>S. nigra</i> Delamare Deboutteville, 1948	Endemic	Central/Ankaratra Massif-Manjakatampo	1600–1800	MFMA–MEF	sH1/f–fM
<i>S. trilineata</i> Delamare Deboutteville, 1948	Endemic	Central/near summit Ankaratra Massif	~2600	MS + MRB	sH1/M
Genus <i>Seira</i> Lubbock, 1869					
<i>S. jacobsoni</i> (Denis, 1929)	+Java	East/Toamasina	~20	Unknown	Hp/b
<i>S. pseudocoerulea</i> Denis, 1929	+Africa	East/Toamasina	~20	Unknown	Hp/b
Genus <i>Lepidocyrtinus</i> Börner, 1903					
<i>L. voeltzkowi</i> (Börner, 1907)	Endemic	Southeast/Ankarimbelo	~500	MFLA	Hh/c
Family Microfalculidae (sensu Szeptycki, 1979)	Endemic				
Subfamily Microfalculinae Massoud and Betsch, 1966	Endemic				
Genus <i>Microfalcula</i> Massoud and Betsch, 1966	Endemic				
<i>M. delamarei</i> Massoud and Betsch, 1966 (type species)	Endemic	North/Montagne d'Ambre	900	MFMA	Hh/c
		+Northwest/Ampasindava Peninsula	300	ShFLA	sH2/b
		+Northeast/Cap Masoala	10	MFLA degraded	Hp/a
Symphyleona					
Family Sminthuridae					
Genus <i>Sminthurides</i> Börner, 1900					
<i>S. sensillatus</i> Massoud and Betsch, 1966	Endemic	Northeast/Maroansetra, beach	~0	Interstitial	Hp/a
Family Katiannidae					
Genus <i>Zebulonia</i> Betsch, 1970 monospecific	Endemic				
<i>Z. massoudi</i> Betsch, 1970 (type species)	Endemic	North/Tsaratanana Massif, south slope	1600–2000	MFMA	Hh–sH1/f–fM
Genus <i>Papirinus</i> Yosii, 1954	East Gondwana				
<i>P. ankaratrensis</i> Betsch, 1974	Endemic	Central/Ankaratra Massif	1700–2200	MEF	sH1/f–M
One or two undescribed species					
Family Sminthuridae					
Genus <i>Sphyrotheca</i> Börner, 1906					
<i>S. madagascariensis</i> Betsch, 1974	Endemic	Central/Ankaratra Massif	2050–2200	MEF	sH1/fM–M
Several undescribed species					
Genus <i>Temeritas</i> Delamare and Massoud, 1963	Pantropical				
<i>T. ambohitantelensis</i> Betsch, 2000	Endemic	Central/Ambositantely	1600	MFMA	sH2/e–f
<i>T. ambrensis</i> Betsch, 2000	Endemic	North/Montagne d'Ambre	900–1100	MFMA	Hh/d

Table 8.21. (continued)

Taxon	Status	Distribution—station within Madagascar	Elevation (m)	Vegetation	Bioclimate
<i>T. ampasimbensis</i> Betsch, 1980	Endemic	Central-east/ Ampasimbe-Analamazaotra	450–1050	MFLA-MFMA	Hp–Hh/c–d
<i>T. andranobensis</i> Betsch, 2000	Endemic	Central/Andranobe Forest	1250	MFMA	sH1/e
<i>T. anjozorobensis</i> Betsch, 2000	Endemic	Central/southeast Anjozorobe	1200	MFMA	Hh/e
<i>T. ankarafantsikensis</i> Betsch, 1980	Endemic	West-northwest/Ankarafantsika	80–200	DDF	S2–S3/b
<i>T. anosyennensis</i> Betsch, 1980	Endemic	Southeast/east slope, Anosyennes Mountains	100–1050	MFLA-MFMA	Hp/c–e
<i>T. antongilensis</i> Betsch, 1980	Endemic	Northeast/Baie d'Antongil, PN de Marojejy	0–700	MFLA	Hp/a–b
<i>T. bergensis</i> Betsch, 1980	Endemic	Northwest/Mampikony–Port Bergé	130–150	DDF	S3/b
<i>T. iarakensis</i> Betsch, 2000	Endemic	Northeast/Iaraka, east slope Masoala Peninsula	500–700	MFLA	Hp/c
<i>T. mahorensis</i> Betsch, 2000	Endemic	North/Mahory, Ankarana	100–200	DDF	S1/b
<i>T. mananteninensis</i> Betsch, 1980	Endemic	Southeast/Manantenina, Analalava Forest	50	MFLA	Hh/b
<i>T. mantasoensis</i> Betsch, 1980	Endemic	Central/east Mantasoa, Andrangoloaka	1350	MFMA	sH1/e
<i>T. marojezensis</i> Betsch, 1980	Endemic	Northeast/PN de Marojejy	500–1300	MFLA-MFMA	Hp/c–e
<i>T. perinetensis</i> Betsch, 1980	Endemic	Central-east/Réserve Spéciale d'Analamazaotra–La Mandraka	900–1200	MFMA	Hh/d–e
<i>T. sahafarensis</i> Betsch, 2000	Endemic	North/Sahafary–Mahory–Ankarana	100–200	DDF	S1/b
<i>T. soalalensis</i> Betsch, 1980	Endemic	West/Soalala, Tongahibe Forest	20	DDF	S2/b
<i>T. tsaratananensis</i> Betsch, 2000	Endemic	North/Tsaratanana Massif, northeast slope	1900	MFMA	Hh/f–fm
Some undescribed species					
Genus <i>Richardsitas</i> Betsch, 1975	Endemic				
<i>R. griveaudi</i> Betsch, 1977	Endemic	West/Marofandilla, north Morondava	10	DDF	sA2/c
<i>R. najtae</i> Betsch, 1975 (type species)	Endemic	South/northeast Amboasary, PN d'Andohahela (parcel 2)	50	DET	sA1/d
Family Bourletiellidae					
Subfamily Bourletiellinae					
Genus <i>Bovicornia</i> Delamare Deboutteville, 1947	Pantropical				
<i>B. cf. greensiadei</i> Massoud and Delamare Deboutteville, 1967	+Salomon Islands	Northeast/Maroantsetra, behind beach	5	Meadow/ Cyperaceae	Hp/a
Genus <i>Massoudia</i> Betsch, 1974 (monospecific)	Endemic				
<i>M. griveaudi</i> Betsch, 1974 (type species)	Endemic	Northwest/Mampikony–Port Bergé	100	Dry savanna	S3/b
Genus <i>Rastriopes</i> Börner, 1906	South tropical				
<i>R. amphygia</i> Börner, 1907	Endemic	Southwest/Andranohinalahy, northeast Toliara	~100–200	DDF–DET	sA3/c
Some undescribed species					
Subfamily Parabourletiellinae Betsch, 1974					
Genus <i>Anjaviidiella</i> Betsch, 1974	Endemic				
<i>A. andoharianensis</i> Betsch, 1980	Endemic	Central/PN d'Andringitra, Plateau d'Andohariana	2100	MPT	sH1/fm–M

(continued)

Table 8.21. (continued)

Taxon	Status	Distribution — station within Madagascar	Elevation (m)	Vegetation	Bioclimate
<i>A. andringitrensis</i> Betsch, 1980	Endemic	Central/PN d'Andringitra, Pic Boby and Pic Bory	2500–2650	MPT	sH1/M
<i>A. anjavidilavensis</i> Betsch, 1980	Endemic	Central/PN d'Andringitra, Anjavidilava	1980–2000	MPT	Hh–sH1/f–fM
<i>A. ankaratrensis</i> Betsch, 1974 (type species)	Endemic	Central/Ankaratra Massif	2300–2600	MPT	sH1/M
<i>A. vohidrayensis</i> Betsch, 1980	Endemic	Central/PN d'Andringitra, Vohidray	2050	MS with <i>Erica</i>	sH1/fM
Many undescribed species					
Genus <i>Bourletiellitas</i> Betsch, 1974 (monospecific)	Endemic				
<i>B. imerinensis</i> Betsch, 1974 (type species)	Endemic	Central/Ankaratra Massif	2000–2100	MEF	sH1/fM
Several undescribed species					
Genus <i>Madecassiella</i> Betsch and Waller, 1996 (monospecific)	Endemic				
<i>M. ibityensis</i> Betsch and Waller, 1996 (type species)	Endemic	Central/south Ibity Massif	1950	MPT, rocky ground	sH1/fM
Genus <i>Parabourletiella</i> Betsch, 1975 (monospecific)	Endemic				
<i>P. mahafalensis</i> Betsch, 1975 (type species)	Endemic	Southwest/Mahafaly Plateau	100	DET	sA3/c
Genus <i>Paulianitas</i> Betsch, 1977 (monospecific)	Endemic				
<i>P. viettei</i> Betsch, 1977 (type species)	Endemic	West/Marofandilia, north Morondava	10	DDF	sA2/c
Genus <i>Vatomadiella</i> Betsch, 1974	Endemic				
<i>V. descarpentriensis</i> Betsch, 1980	Endemic	Central/south Ibity Massif	1950	MRB	sH1/fM
<i>V. pauliani</i> Betsch, 1974 (type species)	Endemic	Central/Ankaratra	2450–2643	On small rocks in MS	sH1/M
<i>V. peyrierasi</i> Betsch, 1980	Endemic	Central/Itrero Massif	1650–1700	MRB	sH1/e–f
Some undescribed species					

NOTE: See table 8.22 for vegetation and bioclimate codes (hydic deficit ranges/minimum temperature ranges).

much more limited geographic range in the southeast. It is known from both moist forests at medium to high elevations, as well as subarid *Euphorbia* and *Didiereaceae* thickets; these are two highly contrasting habitats with very different hydric conditions (fig. 8.16). However, the Poduromorpha do not occur extensively across the western dry and the southwestern and southern subarid portions of the island. Conversely, epigeous Symphypleona have colonized all bioclimate zones, from the hottest to the coldest, from the most humid to the subarid, with species that have differentiated themselves in all possible niches.

Vegetation Types

The Collembola are saprophagous and hence very dependent on the quality of the dead plant matter they ingest. The

Symphypleona, which rely especially on litter, are directly bound to plant formation types through litter types, whereas the Poduromorpha, being more dependant on soil, are indirectly bound to vegetation through humus type. In table 8.21 the associated bioclimate type and vegetation are indicated for all Malagasy Collembola, using the coding system provided in table 8.22. The Symphypleona have extensively colonized the mountainous environments of Madagascar and the dry and subarid bioclimatic sectors. In many cases they are represented by endemic genera that are dependent on particular biotopes—for example, *Zebulonia* in humid forest litter at medium elevation, *Bourletiellitas* in montane humid forest litter, *Anjavidiella* in montane *Erica* thickets, *Madecassiella* in the rocky substratum at ground level within montane *Erica* thickets, *Vatomadiella* in small-sized rocky areas in montane savanna, *Richardsi-*

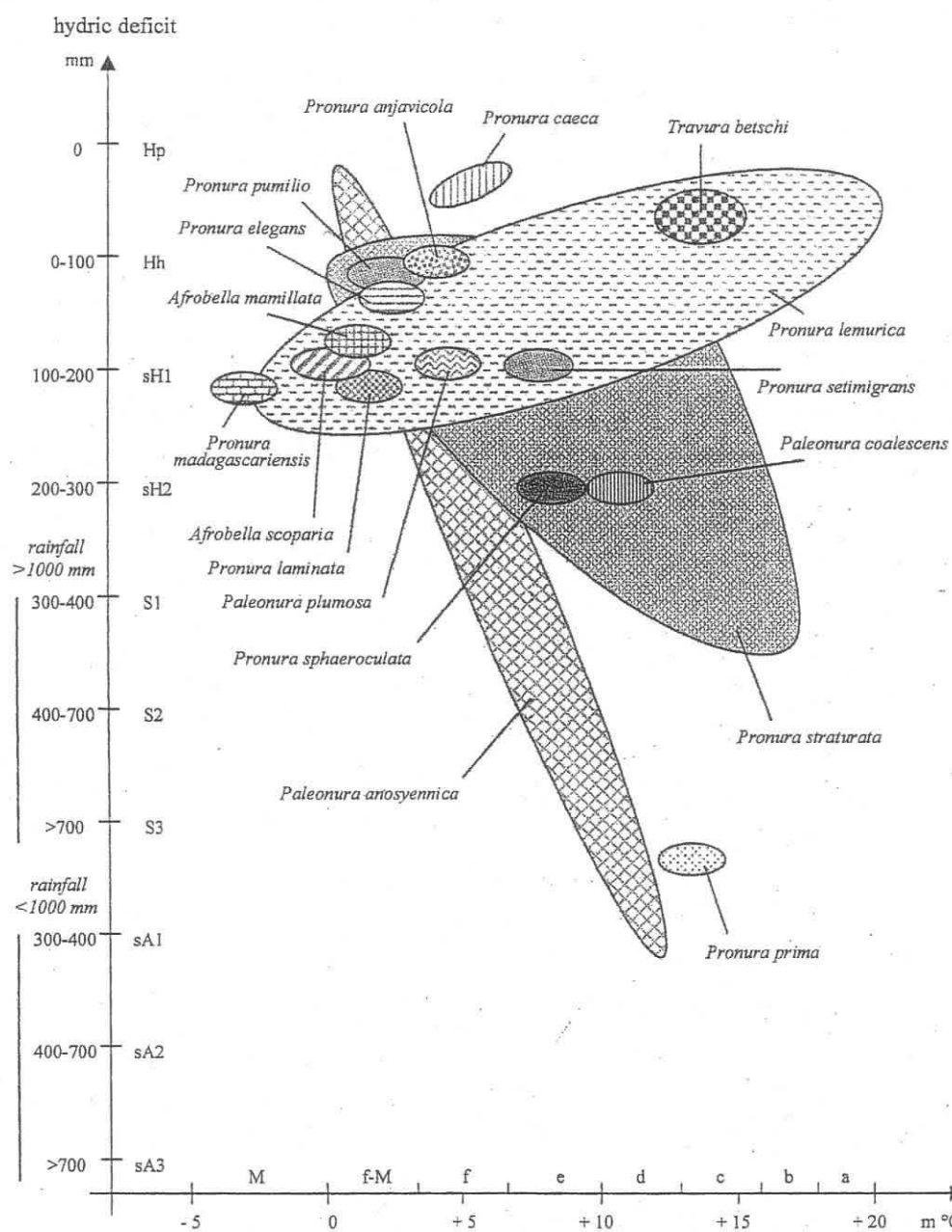


Figure 8.16. The ecological distribution of members of Poduromorpha: Neanurinae based on bioclimatic criteria (see table 8.22).

tas and *Paulianitas* in the litter of dry forests, and *Parabourletiella* on the floor in *Didiereaceae* thicket (fig. 8.17). The *Symphyleona* also represent a wide variety of forms (see fig. 8.18).

In general, Malagasy species belonging to genera with more or less broad distributions in the intertropical zone have not developed ecological adaptations different from those of African or Southeast Asian congeners. For these taxa there appears to be no shift or widening of their niche.

Table 8.20 gives the collection localities visited during the course of my studies on Madagascar and the Collembola species found at each site. The locality numbers correspond to those shown in fig. 8.15. Two sites on mountains, which contain a wide variety of habitats, are clearly richer in species than homogeneous sites; this is particularly true for the Andringitra Massif.

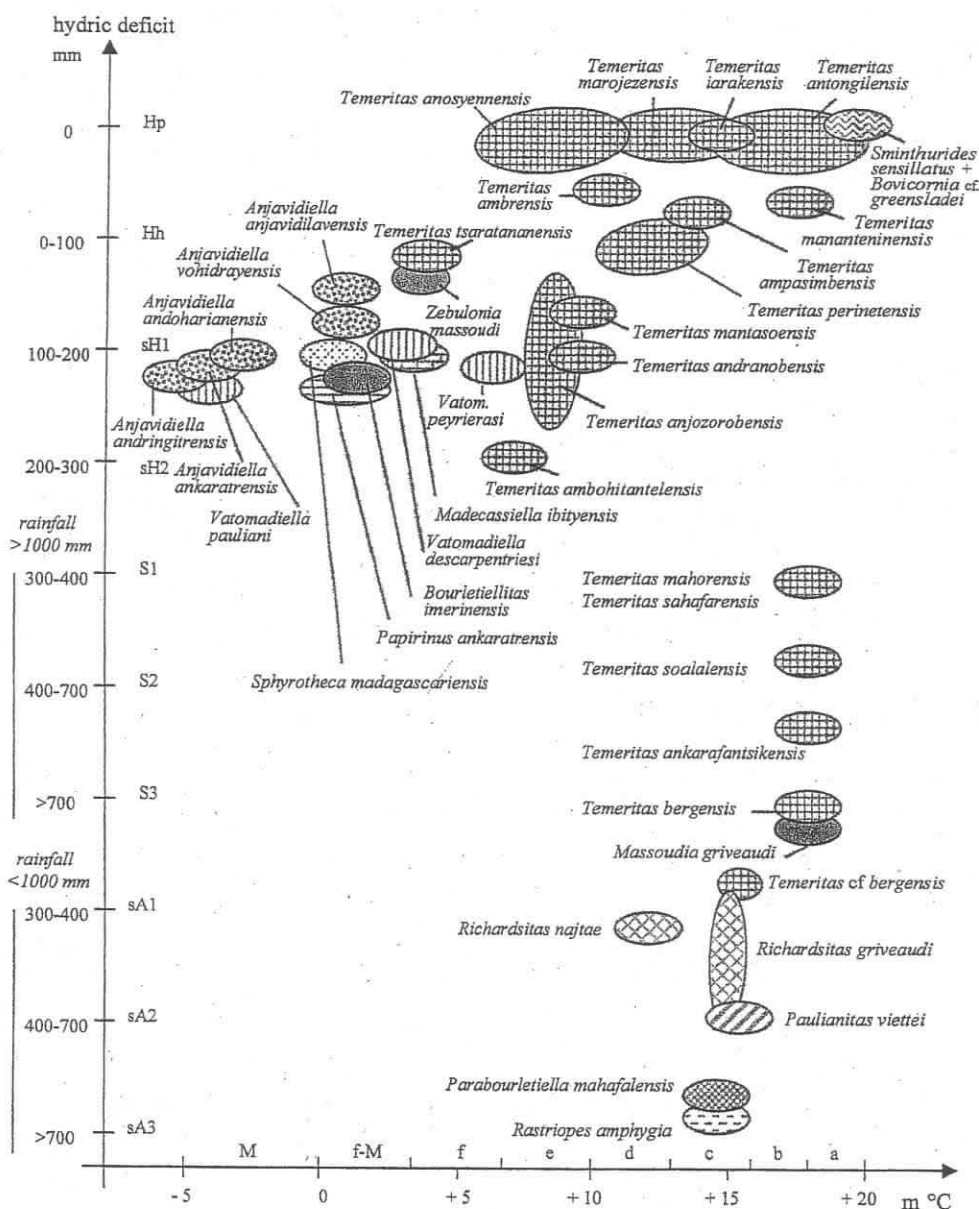


Figure 8.17. The ecological distribution of members of Symphypleona based on bioclimatic criteria (see table 8.22).

Speciation

Except for the well-studied groups Neanurinae and Symphypleona, one cannot actually work out the level of speciation for Malagasy Collembola. Among the Neanurinae, speciation is well marked within the genus *Pronura*. The fairly restricted niche breadth of this genus inhibits colonization of the dry and subarid portions of the island. Among the Symphypleona, two genera have undergone intense speciation. The first is *Temeritas*, a pantropical genus

found in humid and dry forest litter that includes 18 endemic species (table 8.21). At least two or three species remain to be described. Vast portions of the island (especially the west and the south) have not been properly prospected for these animals. Speciation in this genus forms a sort of mosaic—in the east, according more or less to vegetational strata that are divided into three sectors (northern, central, and southern) and then into elevational zones. For example, the central sector at the elevation of Analamazaotra is composed of three levels—*T. ampasimbensis*, <900 m;

Table 8.22. Vegetation and coding for bioclimatic zones

Code	Vegetation type									
MFLA	Moist forest at low altitude (~0–600/800 m)									
MFMA	Moist forest at medium altitude (~600/800–1300/2000 m)									
MEF	Montane evergreen forest									
MscPF	Montane sclerophyllous <i>Erica</i> forest									
ShFLA	Subhumid forest at low altitude (Sambirano area)									
ShFMA	Subhumid forest at medium altitude (in west range)									
DDF	Dry deciduous forest									
MPT	Mountain <i>Erica</i> thicket									
DET	Didiereaceae and <i>Euphorbia</i> thicket									
MS	Mountain savanna									
MRB	Mountain rocky biotope									
Mean minimum temperature (°C) (code)	Hydric deficit codes (mm)									
	Moist		Subhumid		Dry/rainfall >1000 mm			Subarid/rainfall <1000 mm		
	0	0–100	100–200	200–300	300–400	400–700	>700	300–400	400–700	>700
>18 (a)	Hpa						S3a			
16–18 (b)	Hpb			sH2b	S1b	S2b	S3b			
13–16 (c)	Hpc	Hhc		sH2c	S1c				sA2c	sA3c
10–13 (d)	Hpd	Hhd	sH1d	sH2d				sA1d	sA2d	
7–10 (e)		Hhe	sH1e	sH2e				sA1e	sA1e	
3–7 (f)			sH1f							
0–3 (fM)			sH1fM							
<0 (M)			sH1M							

SOURCES: Bioclimate types defined by Cornet (1974); slightly modified by Betsch et al. (2000).

NOTES: Hp, moist/perhumid; Hh, moist/humid; sH1, subhumid attenuated by fog; sH2, subhumid not attenuated by fog; S, dry; sA, subarid. The mean minimum temperature is the mean minimum for the coldest month of the year.

T. perinetensis, 900–1250 m; and *T. mantasoensis*, 1250–1350 m. In the Anosyennes Mountains (southern sector) the strong topographic relief decreases the limit of *Temeritas* in the moist forest at low elevation down to 100 m. In the west, the mosaic pattern is associated with a pronounced pluviometric gradient and the role of rivers between dry areas. The number of species within this genus is estimated to be between 30 and 40. The ecological heterogeneity of Madagascar is partially responsible for the presence of more than half of the world's known species of *Temeritas*.

The second genus is *Anjavidiella*, an endemic group dependent on *Erica*, and it is known only from the Andringitra and Ankaratra Massifs. On Andringitra (see Rasolonandrasana and Grenfell, this volume), three species (*A. andoharianensis*, *A. anjavidilavensis*, and *A. vohidrayensis*) occur in various portions of the ericoid zone just above the

forest line (1900–2000 m) and on different slopes or in different ecological situations, and the fourth species (*A. andringitrensis*) is found in the summital zone at 2500–2650 m, in a very cold subhumid bioclimate. On Ankaratra, the only described species, *A. ankaratrensis*, coexists with an undescribed species that has differentiated itself on *Erica* with different growth habits. Speciation of *Anjavidiella* on Madagascar seems as explosive as that of *Erica*.

Affinities

The ancient origin of the Collembola makes them an interesting group for identifying the affinities of the Malagasy fauna with other Gondwana faunas. The Poduromorpha: Neanurinae of Madagascar, of the Paleonurinis, belong to

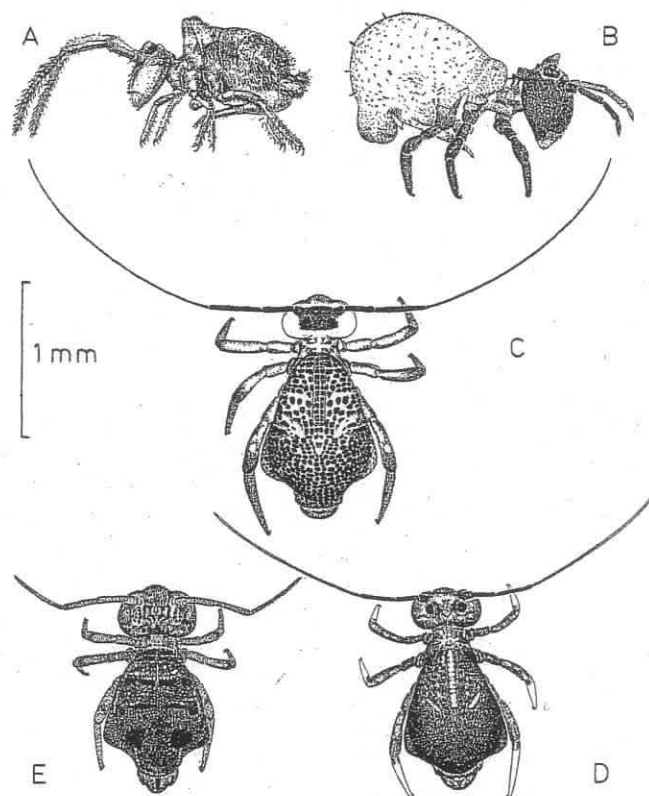


Figure 8.18. Habitus of some Symphypleona: (A) *Zebulonina massoudi*, (B) *Papirinus ankaratrensis*, (C) *Temeritas anjozorobensis*, (D) *Richardsitas najtae*, and (E) *Anjaviidiella ankaratrensis*.

a pantropical "primitive contingent" (*Paleonura*, *Pronura*, and *Afrobella*) composed of endemics very close to African and Asian species; four genera, three of which are endemic (but undescribed) and *Travura*, descended from this contingent (Cassagnau 1996). The Symphypleona include seven pantropical genera, of which four are primitive ancient forest forms (*Collophora*, *Sphyrotheca*, *Pararrhopalites*, and *Temeritas*) and three are recently derived genera (*Calvatomina*, of secondary forest, and *Denisiella* and *Bovicornia*, in open habitats on laterite or Quaternary coastal alluvia). Further, the Symphypleona include two ancient genera also present in Asia and Africa (*Papirinus* and *Afrosminthurus*); some cosmopolitan genera; an Oriental genus that has very likely been introduced to Madagascar (*Papirioides*, with a nonendemic species occurring in secondary forest); one southern genus (*Rastriopes*); and nine endemic genera, six of which may have descended from a southern ancestor.

Conclusion

A Collembola fauna that has a medium level of endemism for genera and high levels of endemism for species characterizes Madagascar. There are several important gaps in the island's fauna with regard to pantropical areas. These include the Poduromorpha: Neanurinae of the Paranurini and Lobellini tribes, which are known only from the Oriental region; and among the Symphypleona, the genera *Stenognathriopes* (Africa, Southeast Asia) and *Neosminthurus* (eastern Africa, Oriental region, and South and Central America). The level of speciation varies among the genera. It is well developed for one genus within the Neanurinae, explosive for two Symphypleona genera (one of which is pantropical and the other endemic), and relatively restricted for most other genera. Major voids exist in our current knowledge of Malagasy Collembola, particularly in the west, the south, and zones with considerable relief.